Why Are There So Few Butterflies In The High Andes?

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Abstract. The high Andes have a depauperate butterfly fauna even though they are adjacent to the faunistically rich Amazonian lowlands. Andean oreal butterfly faunas are impoverished even as compared to the mountains of California. There is a tradition of attributing the high-Andean fauna to Holarctic lineages which colonized South America in the Great American Interchange some 2-3 million years ago. Most of the critical taxonomic relationships are too poorly resolved to separate common ancestry from convergence, but in at least the Thecline Lycaenids cladistic studies strongly support convergence. Unusual aspects of the Andean and Patagonian butterfly faunas (including relationships between the tropical Andes and the temperate south, host-plant relationships, and the dominant position of the Pronophiline Satyrids) are reviewed and placed in both biogeographic and paleogeographic contexts.

The richness of lowland Neotropical butterfly faunas is proverbial. The famous latitudinal gradient in biodiversity is not, however, repeated in the butterflies of very high altitudes in the Neotropics. As a result, the latitudinal gradient in biodiversity is oversteepened in the New World tropics relative to temperate latitudes. Equatorial Andean butterfly faunas are both absolutely and relatively impoverished in comparison to both temperate oreal (high-mountain) faunas and adjacent lowland ones. Why should this be so?

The diversity of any high-altitude biota should in theory be related to at least the following factors: (i) the antiquity of the environments in question, (ii) the availability of preadapted biota to colonize them in ecological time, (iii) the availability of sources of potential colonizers which could adapt to oreal conditions in evolutionary time, and (iv) the area of the environments (in terms of species-area relationships).

The oreal butterflies of the Andes and the Sierra Nevada of California, the great mountain ranges of the far west of South and North America respectively, may be compared instructively from a biogeographical standpoint. The comparison is not, however, without problems. Both are generally considered young mountain ranges, achieving their present heights and first presenting the opportunity for the development of an oreal biota in Plio-Pleistocene time. [Molnar and England (1990) have challenged this conventional wisdom. Their position, if correct, would force the re-evaluation of virtually all existing scenarios in montane-oreal biogeography. For purposes of this paper, the conventional assumptions about the ages of the Andes and Sierra Nevada will be accepted.] In

both ranges, the emergence of alpine environments coincided temporally with the climatic instability of the Pleistocene, with its repeated episodes of glaciation. The climatic and vegetational histories of both in the Quaternary are fairly well documented, though the record for both the northern Andes (work of Van der Hammen and Cleef) and the far south (Patagonia and Fuegia; work of Auer, Mercer and others) (see references in Shapiro, 1991a) is denser, more continuous, and in general more satisfactory than what is currently available for the Sierra Nevada (Heusser and King, 1988; Fullerton, 1986). A very detailed picture is emerging for the late Quaternary of forested, humid Chile (Ashworth and Hoganson, 1993) which is unfortunately not very useful for butterflies, since the butterfly fauna of these climates is so poor.

Area comparisons are difficult. The Andes are not a single mountain chain, but a huge complex extending from 10° N to 54° S Latitude, incorporating a vast area of high plateaux, the Peruvian-Bolivian *altiplano*. The northern Andes are often humid or at least seasonally so; farther south occur various semiarid to extreme desertic regimes, and still farther south the cool-temperate rain forests of archipelagic Chile. The Sierra Nevada is much more modest in scale. Although it is sometimes considered the world's longest single continuous mountain chain, it demonstrates little north-south climatic differentiation in comparison to the Andes — but then, it is confined within a latitudinal range from 40° to 36° N. Climatically, the oreal Sierra Nevada is most directly comparable to the corresponding sector at the latitude of Mendoza, Argentina, south to northernmost Patagonia (33-44° S). At these latitudes the Andes separate the Mediterranean climate of the Chilean Central Valley from the more continental climate of the Argentine *monte* (high desert), just as the Sierra stands between the Mediterranean climate of the California Central Valley and the continental desertic or subdesertic climate of the Great Basin in Nevada. A better latitudinal comparison would include the North American Cascades, Coast Ranges, and some of the Alaskan mountains, but detailed butterfly faunistic information was not available for this purpose. The relationship of the Mexican montane (virtually no oreal) butterfly faunas to those of the lowland tropics is complex enough to warrant entirely separate consideration.

The high altitudes of the Andes embrace a variety of oreal vegetation formations, variously called *páramo* (humid to semiarid) in the north,

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Plate I.   Upper left: South Andean - Patagonian small fritillaries (*Yramea*) (top two rows) and their Boreal counterparts (*Clossiana*). Both groups feed on Violaceae and Rosaceae, but is this indicative of relatedness or merely another level of convergence? Upper right: Undescribed *Yramea* (near *inca*) from northwestern Argentina, showing male "green" melanization convergent to sympatric *Colias blameyi* and to the Boreal *Clossiana improba*. Lower: upper- and undersides of male *Baltia* from Gyaco La, Tibet (5250m) (above) and *Phulia* from Cordón del Viento, Argentina (3700m).

jalca (humid or subhumid) in Peru, and *puna* and *altiplano* (mostly semiarid to arid) in Peru, Bolivia, Chile and Argentina. In the Southern Cone the oreal belt dips ever lower as one progresses south, and south-end-of-the-world taxa become increasingly prominent in the flora. The Andean oreal communities differ tremendously in floristics, faunistics, aspect and seasonality, though a surprising number of plant and animal genera span much of this latitudinal diversity. By contrast, the Sierra Nevada oreal zone is relatively uniform, with a gentle north-south climatic gradient; the most dramatic floristic (and butterfly-faunistic) differences are often defined edaphically rather than latitudinally.

Defining the oreal zone is somewhat arbitrary in those parts of the Andes (as well as in the eastern Sierra Nevada) where there is no "tree line" because there are no trees. In parts of the northern Andes, more-over, deforestation has led to a downslope migration by *páramo* vegetation into land formerly occupied by the upper cloud forest. Any quantitative analysis of species-area relationships must also correct the area of oreal communities for the degrees of latitude spanned, and perhaps for other things. All these complications raise doubts about pursuing this approach; the trend, in any case, is obvious and unlikely to be greatly elaborated by such analyses.

The matter of source regions for potential colonizers is critical for our comparison. The Andes directly adjoin the world's greatest center of biodiversity — Amazonia — and one normally assumes that the lowland habitats and communities are older than their highland neighbors: Amazonia is thus the most obvious source for potential high-altitude colonizers, and the butterfly diversity of Amazonia is the world's highest. Butterfly diversity in areas near the Sierra Nevada and likely to contribute to its oreal fauna is an order of magnitude lower. By the time the Sierra had reached alpine heights, access to the humid-neotropical Tertiary biota had been shut off. Indeed, the rise of the Sierra itself administered the *coup de grâce* by altering the rainfall patterns in ways hostile to that biota. Any emerging Sierran oreal biota would henceforth be recruited from what may be broadly characterized as Madro-Tertiary and Arcto-Tertiary sources. (These terms are used loosely, since recent paleovegetational scenarios, e.g., Wolfe, 1985, are considerably more complex than the classic formulation by Axelrod.) At any rate, if we assume that all lowland lineages have an equal initial probability of colonizing the oreal zone (obviously untrue), many more lineages are available to the tropical Andes than to the Sierra Nevada. *Ceteris paribus*, there should be much more butterfly diversity in the tropical than the Sierran oreal zone. And there is not.

If we consider just ecological time, species preadapted to the physiological rigor of life in the oreal zone might be assumed to be more readily available to the Sierra Nevada. However, this is not absolutely certain. Mercer and Sutter (1982) and Clapperton (1983) suggest that glaciation began in southern Patagonia some seven million years ago, more or less

contemporaneously with the first hints in Alaska. Thus, a cold-adapted butterfly fauna could have existed in the far south of South America, moving north up the spine of the Andes like the Austral flora. However, this presupposes the existence of any Austral butterfly fauna that far back. If there was a Patagonian butterfly fauna, it must have been very undiverse. (There is no paleontological or convincing biogeographic evidence for the existence of an Austral butterfly fauna prior to the breakup of Gondwanaland.) In the large and diversified Laurasian land mass, butterflies would have had much more opportunity to adapt to continental climates than in the Southern Cone of South America; both Arcto- and Madro-Tertiary species might be expected to be better adapted to emerging oreal conditions than lowland tropical ones would be, as discussed later.

How Good are the Data?

There is no Andean oreal butterfly fauna that can be considered truly well-known. This is particularly true of the tropical Andes, where most collecting has been done by transient visitors in an unsystematic way, at random and often inappropriate seasons. The seasonal component of butterfly diversity is very poorly understood in the high Andes. Most of the collecting has been done along trans-Andean highways, and therefore emphasizes the faunas of plant communities found in and near passes. Many habitats have never been collected at all. Thus all the Andean data must be considered provisional. The only attempt to date to collate such information is Descimon's (1986), using in part the antique data of Fassl (various publications cited in Descimon, *loc. cit.*) as well as his own field experience. Descimon tabulates "oreal faunas" from the Sierra Nevada de Santa Marta in the far north (Colombia) to southern Tierra del Fuego, ranging from two (Santa Marta) to 35 ("S Peru") species. There is at least a crude suggestion of a double cline of species richness here, which cannot be rationalized by latitude but might be on other grounds. However, the data are very unreliable. The largest faunas are large-scale territorial composites ("S Peru," "Bolivia") while the smallest (Santa Marta, Cordillera de Mérida, Tierra del Fuego) are much smaller in both extent and ecological diversity. (The Sierra Nevada de Santa Marta is actually not even part of the Andes.) The definition of "oreal" here is also disturbingly vague. There are no butterflies in the oreal zone in southern Patagonia and Fuegia, if that zone is defined as being above the tree line. (Two species — *Yramea cytheris* and *Hyposchila microdice* — make it just to tree line in the Cordillera Martial behind Ushuaia.) The Patagonian fauna enumerated by Descimon (eight species) does not match any Patagonian fauna I have seen. It omits the rich Satyrid fauna (surprisingly, since this fauna has been monographed), the unexpectedly speciose hairstreaks (not surprisingly omitted since most of the species were still undescribed in 1986, and many still may be), and the blues, but includes *Colias lesbia*, which is resident only along the Gulf

of San Jorge in the south; yet it leaves out *Tatochila autodice* and *T. vanvolxemii*, whose Patagonian ranges match that of *C. lesbia*. And the Sierra Nevada de Santa Marta fauna omits 50 percent of the recorded butterfly species (*Reliquia santamarta*, referred to elsewhere in Descimon's paper!, and an at-that-time unnamed hairstreak). And all of the faunas omit the Hesperiidae altogether.

These are definitional problems, oversights, or results of lack of communication. There is a more profound problem underlying any such analyses, however, and that is sheer ignorance. Even in the temperate Argentine Andes, the alpine faunas cannot be considered well-known. The biogeographically important species *Colias mendozina* was collected twice near the turn of the century and then lost until 1989, when I rediscovered it — ten minutes' walk from the transandean superhighway connecting Argentina and Chile at Las Cuevas! The Lycaenid fauna of the same area (the Aconcagua Provincial Park, collected — albeit sporadically — for over a century) was largely undescribed before 1992. Slightly farther north, the "Chilean endemic" *Colias flaveola* was just discovered in 1988 living happily on the Argentine side of the crest in the Province of San Juan. If this sort of thing is routine in the best-collected and most accessible Andean oreal fauna, what must be true farther north? Although a Lycaenid sibling species new to science has just been recognized in the Sierra Nevada oreal fauna (J.F. Emmel, pers. comm.), the overall situation is clearly much better in California than in the Andes. Thirty years ago little of the high country had been collected and many common, widespread oreal species were thought of as rare and very localized. Now, however, there has been plenty of collecting in midsummer near the accessible passes, and a respectable amount in more remote areas. The beginning and end of the season are less well-documented, although it is unlikely any more new species are to be found then (for the same reason as collectors rarely venture in at such seasons: the weather is too unpredictable for butterflies to count on flying then). Some Sierran oreal areas become snowfree in spring before the forested regions below, and are accessible only on skis or snowshoes during the first few weeks of the flight season. Because many species emerge quickly after snowmelt, this renders our phenological data at least less than ideal. It is, however, safe to say that the broad outlines of Sierran butterfly faunistics are now well-defined and major surprises are unlikely.

Plate II. Above: Holarctic (left) and South Andean - Patagonian (right) Satyridae of steppe and tundra habitats. All the South American taxa are Pronophilini; the Holarctic ones are Maniolini and Erebiini. Below: Repeated evolution of "green" *Colias* phenotypes in cold climates. Each pair represents a different sublineage, and the non-green specimen is the postulated closest relative of the greens; all are males. Top: *C. behrii* (California) and *C. palaeno* (circumpolar). Center: *C. nastes* and *C. hecla* (both Alaska). Bottom: *C. weberbaueri* and *C. euxanthe* (Bolivia).

In selecting sites for comparison, both Andean and Sierran, I have emphasized accessibility and completeness of coverage. The data (Tables 1, 2) are striking — just as striking, in fact, as Descimon's. It is almost certainly biologically significant that all of the northern Californian oreal faunas are richer than any of the Andean ones, which run from 10° N (Sierra Nevada de Santa Marta) to the temperate Paso Bermejo at the Aconcagua Provincial Park (33° S). Moreover, the impoverishment in species in the Andean faunas is mirrored by their impoverishment in lineages; it is unlikely that other groups will duplicate the recently-discovered richness of the Lycaenid fauna discussed below, because among the butterflies the Lycaenids seem uniquely prone to philopatry, intense host specialization, and cryptic speciation.

Origins of the Sierran Oreal Fauna

In a very important paper, Chabot and Billings (1972) demonstrated that the largest contributor to the constitution of the Sierran oreal flora was the Great Basin. This is a flora already adapted to intense winter cold, intense insolation, and a general water deficit year-round, albeit with summer rain. A substantial number of plant species, such as Bitterbrush (*Purshia tridentata*, Rosaceae), Sagebrush (*Artemisia* spp., Compositae), and Daggerpod (*Phoenicaulis cheiranthoides*, Cruciferae) are equally at home in high desert and at tree line. The same is true of several butterflies, such as *Lycaena heteronea*, *Euphilotes battoides*, *Satyrium fuliginosum*, *Lycaeides melissa* (all Lycaenidae) and *Pontia occidentalis* (Pieridae). (Of these, *L. melissa* alone is suspected of being more than one genetic species.) The Sierra has the smallest percentage of circumpolar relict plants in its oreal flora of any northern-hemisphere mountain range so far from the Equator. Pleistocene conditions undoubtedly shaped the access of such elements (represented conspicuously by Mountain Sorrel, *Oxyria digyna*, Polygonaceae) to the Sierra. They could have come from the north, northeast or east (across the Great Basin from the Rockies, see below; the "Convict Creek flora" of Major and Bamberg, 1967 is the classic argument for cross-Basin dispersal, subsequently reinforced by studies of pack rat middens (Betancourt et al. 1990)).

Most butterfly taxa of the Sierran oreal zone are conspecific with Rocky Mountain taxa, and the subspeciation in most cases is weak. The Rocky Mountain fauna has been attenuated by distance, but also by extinctions in the Xerothermic (Hypsithermal). During this warm interval a few thousand years ago, cold-adapted organisms were driven to extinction in the low northern Sierra north of Donner Pass, resulting in disjunctions between the northwest California (Klamath-Trinity-Siskiyou-Eddy) and central and southern Sierran oreal zones. The most famous of these is Foxtail Pine, *Pinus balfouriana*. The most important Rocky Mountain oreal element conspicuously missing from the Sierran fauna is the genus *Erebia* (Satyridae). Moreover, the taxonomic distance between the Sierran oreal butterfly fauna and the adjacent low-elevation faunas is not

Table 1. Oreal Butterfly Faunal Composition

	Trinity Alps[a]	Mt. Eddy[a]	Castle Peak[b]	Carson Pass[c]	Yosemite[d]
Satyridae	0	0	2	3	2
Nymphalidae	12	11	10	19	13
Lycaenidae					
Theclinae	3	2	4	6	2
Lycaeninae	3	3	5	5	7
Plebeiinae	9	9	9	14	10
Riodinidae	1	1	0	0	0
Pieridae					
Euchloinae	2	1	3	2	1
Coliadinae	1	1	1	1	2
Pierinae	2	2	2	2	2
Papilionidae	4	4	4	5	4
Hesperiidae					
Pyrginae	2	2	4	3	1
Hesperiinae	4	4	4	4	5
Totals	43	40	48	64	49

	Sierra Nevada de Sta. Marta[e]	Morococha-Ticlio[f]	Cumbres Calchaquíes[g]	Paso Bermejo[h]
Satyridae	0	2	5	5
Nymphalidae	0	2	5	4
Lycaenidae				
Theclinae	1	3	4	3
Plebeiinae	0	1	3	3
Pieridae				
Coliadinae	0	3	3	2
Pierinae	2	5	8	3
Hesperiidae				
Pyrginae	0	2	2	1
Hesperiinae	1	3	3	0
Totals	4	22	33	21

Notes: Strictly migratory or casual spp. omitted from all tallies. [a]Shapiro, Palm & Wcislo 1981. [b]Shapiro 1978 + unpublished. [c]Shapiro, unpubl. data 1972-90. [d]Garth & Tilden, 1963 + unpublished from various sources. [e]Colombia, Dept. Cesar, above 3500m. [f]Peru, Dpto. Junín, above 4400m. [g]Argentina, Prov. Tucumán, above 3000m. [h]Argentina, Prov. Mendoza, above 2700m. [e-h]Shapiro, unpublished data + data from other sources.

Table 2. General characteristics of oreal butterfly faunas in North and South America and their regional affinities.

Some Important Andean Oreal Butterfly Genera			
	In Holarctic oreal?	In lowland Neotropics?	In Patagonia?
Hesperiidae			
Pyrgus	Yes	Yes	Yes
Hylephila (*boulettii* group)	No	Yes	Yes
Pieridae			
Colias	Yes	No	Yes
Tatochila	No	No	Yes
Hypsochila	No	No	Yes
Phulia	No, but cf. *Baltia*	No	No
Pierphulia	No	No	No
Piercolias	No	No	No
Infraphulia	No	No	No
Reliquia	No	No	No
Lycaenidae			
"*Itylos*" sensu lato	No	No	Yes
Eiseliana	No	No	No
Penaincisalia	No	No	Yes
Nymphalidae			
Yramea	No, but cf. *Boloria*	No	Yes
Vanessa (seasonal migrants?)	Yes	Yes	Yes
Satyridae			
(various Pronophilini)	Entire tribe absent	Yes	Yes

Some Important Sierran Oreal Butterfly Genera			
	In Andean Region?	In Great Basin?	In Rocky Mountain Oreal?
Hesperiidae			
Pyrgus	Yes	Yes	Yes
Hesperia	No	Yes	Yes
Pieridae			
Pontia	No	Yes	Yes
Colias	Yes	Yes	Yes
Lycaenidae			
Lycaena	No	Yes	Yes
Agriades	No	Yes	Yes
Lycaeides	No	Yes	Yes
Nymphalidae			
Boloria + *Brenthis*	No, but cf. *Yramea*	(Yes)[a]	Yes
Satyridae			
Oeneis	No	Yes	Yes
Neominois	No	Yes	(Yes)[b]

Notes: [a]Only in montane habitats. [b]Present mostly below the oreal zone in the Rockies.

striking. All of the oreal species have lower-elevation congeners nearby
(except *Neominois* which only goes lower much farther east), and a rather
large number of oreal species extend some distance below tree line as
well. There is none of the sense, described by Descimon for the Andes, of
entering a different world when one passes from the montane to the oreal
fauna.

The oreal butterflies of far northern California (which has only tiny
areas of climatically treeless highlands) are a southward extension of the
Cascadian fauna. They are much less like the Rocky Mountain fauna
than is the Sierran one. The oreal-endemic Sierran *Oeneis* (*ivallda* and
stanislaus) present the strongest case for cross-Basin dispersal (Porter
and Shapiro, 1990). To the contrary, the Fritillary *Speyeria mormonia*
connects up its Cascadian and Sierran subspecies via a series of small,
relict populations (Mount Eddy, Ball Mountain, Warner Mountains)
which constitute our best butterfly evidence so far of a northerly access
route, though by no means conclusive.

Although North America acquired some butterfly taxa in the Great
American Interchange of flora and fauna which commenced some three
million years ago (Stehli and Webb, 1985; Simpson, 1980), the impact on
the Sierran alpine butterfly fauna was nil; specifically, no Andean
butterflies appear to have colonized the Sierra. One Andean butterfly
(*Nathalis iole*, which is a montane or oreal species in Colombia, not noted
by Descimon) did successfully occupy North America — but in desert,
montane and warm-temperate, not oreal communities. Only one Sierran
oreal species (*Thorybes mexicana* ssp.) is even of Madro-Tertiary prov-
enance! Otherwise, the Sierran oreal fauna is ultimately all Arcto-
Tertiary or derivative therefrom.

The genus *Pyrgus* (Hesperiidae) is of special interest because it has
speciated in the Andes and Patagonia to a greater extent than in North
America, and several of its species are oreal. No phylogenetic analysis of
Pyrgus has been done, but superficially it does not appear that there has
been any communication in either direction between the western North
American and the Andean oreal *Pyrgus* faunae. The large Andean
Hesperiid genus *Hylephila*, with several important oreal taxa from the
Sierra Nevada de Santa Marta to Patagonia, apparently entered lowland
North America as the subtropical weedy species *H. phyleus* in or after the
Great American Interchange, but never penetrated the mountains.

ORIGINS OF THE ANDEAN OREAL FAUNA

The Andean oreal faunas are derived from a remarkably small number
of lineages, probably fewer than 20, most of which have been attributed
by most authorities to invasion from the north at the time of the Great
American Interchange. If this notion is correct, the imbalance is very
striking: northern invaders allegedly defined the entire Andean oreal
fauna, while southern ones had zero impact in the Sierra Nevada.

The notion of a northern origin for the Andean oreal fauna originated in the 19th Century. Initially many Andean species were described in Palearctic genera, based on superficial, but often strong, resemblances in habitus. Eurocentrism and a subsequent analogy between the migrations of *Homo sapiens* and the supposed migrations of butterflies in geologic time colored subsequent phylogenetic speculation. Dixey (1894, pp. 322-326), for example, wrote:

> In the Chilian or Andesian division of the Neotropical Region we find the genus *Tatochila*, which appears not to belong to the regular Neotropical Pierine stock, but to be closely related to the Palearctic *Pontias*. It is conceivable that the latter stem may have spread from Asia into the western portion of the Nearctic continent, and thence down the mountain chains to the south... Another indication of the same invasion is afforded by the genus *Phulia*, now found with the nearly-allied *Tatochila* only in the Andesian or Chilian Subregion, to which it no doubt made its way along the great mountain chains in a similar manner. Its close ally *Baltia* remains in the high lands of Central Asia, where it bears much the same relation to *Synchloe* as *Phulia* to *Tatochila*... The earliest species of *Synchloe* were undoubtedly differentiated from *Pontia* or *Baltia* in the Palearctic Region, from which the genus spread (probably eastwards) into the Nearctic.

This is in keeping with the attitude reflected in a famous quote from Wallace (1876):

> The north and south division of the modern biota represents the fact that the great northern continents are the seat and birthplace of all the higher forms of life, while the southern continents have derived the greater part, if not the whole, of their vertebrate fauna from the north...

Dixey's scenario was repeated by Klots (1932), Mani (1968), and even Descimon (1986, p. 526), who wrote:

> In summary, it is clear that the Neotropical and southern temperate regions contributed little (or nothing) to the oreal butterfly fauna of the Andes. Its affinities lie instead with the Holarctic realm.

This is certainly in keeping with the traditional viewpoint of plant geographers, who noted early the conspicuous predominance of Holarctic plant lineages above the Andean tree line. Such genera as *Castilleja* (Scrophulariaceae) and *Lupinus* (Leguminosae) are conspicuous elements in the northern Andean *páramos*; they are clearly of northern provenance and diminish in importance southward, as one would expect if they were fairly recent arrivals. With striking symmetry, most of the lowland plant diversity — and with it, most lowland tropical plant lineages — disappears at tree line. The turnover in floristics was attributed by Walter and Medina (1969) to the difficulty in acclimating evolutionarily to the diel thermal regime in the *páramo* — with daily

maxima as high as 15-20 °C but nightly minima below freezing most nights of the year.

If the Andean oreal regime arose at about the same time as the Great American Interchange, it can be argued, Holarctic cold-adapted plants travelling by sweepstakes dispersal would probably arrive before many lowland-tropical plants could have adapted to highland conditions. These plants, and the cool-adapted Austral flora migrating north from Valdivia, would then have competitively locked up the oreal zone and prevented much penetration from the lowland floras. In turn, the Holarctic butterflies, preadapted to feed on Holarctic plants, would have followed them south. The lowland butterfly fauna, with no coevolution-ary history of dealing with Holarctic plants and their phytochemistry, would have been deterred if not excluded from the highlands. This is essentially Descimon's scenario. It is in the great tradition of narrative biogeography: seductive, plausible, and difficult to falsify. Descimon's argument has been falsified for one lineage, the hairstreaks (Theclini or Eumaeini, Lycaenidae). Kurt Johnson and his collaborators have shown that the various high-Andean and Patagonian hairstreaks, mostly undescribed or known from very few specimens, and treated by most workers including Descimon as of Holarctic affinities, are merely conver-gent in phenotype to Holarctic hairstreaks (Johnson 1991a,b; Johnson, Miller & Herrera 1992). They really are derived from the lowland-tropical hairstreak fauna. This is true of both the "Andean *Incisalia*" and the characteristic genus *Eiseliana* of the Argentine *puna*. Furthermore, most of the hairstreak genera represented in the high-Andean fauna have congeners in Patagonia, and most are richer in the south than in the north. One of Johnson's new genera has species from oreal Colombia to the Argentine province of Chubut. (This repeating pattern is the same as that seen in the Pronophiline Satyrids, discussed further below.)

Are any other components of the oreal fauna likely to be re-evaluated in this way? There has been an explosion of interest in the Andean blues (Lycaenidae, Polyommatini) resulting in unfortunate taxonomic confu-sion (Balletto, 1993; Bálint and Johnson 1993a,b; Bálint 1993). Their greatest richness is in northern and central Argentina, Bolivia and Chile. The work of these authors has demonstrated convincingly that the previous appearance of low diversity in these blues was illusory. The ranges of most of the newly-recognized species are very poorly known, and it is not obvious whether geographic or ecological replacement, seasonal allochrony, or sympatry and synchrony properly define the structure of all this richness. Nor has the phylogenetic position of the Andean fauna — along with its geographic relationships — yet been defined. To do so is urgent, especially vis-à-vis the Asian oreal and steppe fauna.

Meanwhile, Lee Miller (pers. comm.) has revised his opinion of the Pronophilini, incorporated by Descimon in his scenario. Miller now believes that the family Satyridae is of Gondwanian origin (no later than

early Cretaceous, obviously) and only entered the Northern Hemisphere by riding India into the underbelly of Laurasia. By this scenario, the Pronophilines are primitively autochthonous in South America. When we recall that the oldest butterfly fossils are only Oligocene, it is evident that the days of extreme conservatism in blaming everything on the Pleistocene and the Great American Interchange are over. The danger now is of over-reaction — of projecting butterfly evolution back into the Devonian, if not the Pre-Cambrian.

FURTHER CONSIDERATION OF THE PIERIDAE

Descimon focuses especially on the Pierini and the genus *Colias*. Let us consider *Colias* first. Again, our modern scenario reflects Dixey, 1894 (pp. 326-327):

> No other genus in the whole subfamily has so extensive a range as *Colias*... Here again, I have little doubt that the site of original divergence is Asiatic... after populating the Palearctic and Nearctic continents with numerous species [it has] passed down the great mountain chains of Central and South America to Chili and Patagonia, and has even established outposts in Venezuela and the Sandwich Islands (the occurrence of *Colias* in the last-named locality is, however, not entirely free from doubt).

All taxonomists but Berger (1988) have treated the Andean *Colias* implicitly as a monophyletic group, displaying little morphological change but great adaptive radiation in color, pattern and sexual dimorphism which more or less duplicates what occurs elsewhere in the world. (There has been no global cladistic analysis of *Colias* — perhaps surprisingly.) *Colias* is overwhelmingly a Holarctic genus, with greatest diversity in Asia both in terms of species and species-groups. Hardly any *Colias* occur in forests; they are steppe insects *par excellence* and their current distribution in the Holarctic shows the influence of the periglacial steppe-tundra. Most of the species whose life-histories are known feed on Papilionaceous legumes, especially *Vicia*, *Lathyrus*, *Trifolium*, *Astragalus* and related genera. In the Holarctic there are small groups of willow-(Salicaceae) and Ericaceae-feeding species (more diverse in the Nearctic than in the Palearctic). The southernmost Ericad feeder, *C. behrii*, is endemic to the central and southern Sierra Nevada, probably of Pleistocene origin and derivative of *C. palaeno* (or perhaps *C. pelidne*).

The Andean *Colias* reared to date are all Papilionaceous-Legume feeders. Most of them now routinely breed on naturalized clover (*Trifolium repens*) and/or alfalfa (*Medicago sativa*) and in a few cases have yet to be found in anything else. They seem most closely related to the legume-feeding Holarctic group that includes *C. hecla*, but this remains to be rigorously demonstrated. This is mainly a boreal group, with oreal relict populations south to the central Rocky Mountains. The southernmost Nearctic *Colias*, *C. philodice* and *C. eurytheme*, reach Guatemala but belong to a different group unlikely to be closely related to the Andean

species. Andean species apart, the only other Southern Hemisphere *Colias* is *C. electo*, with a scattered, relictual distribution in South Africa and montane tropical Africa and clearly of Palearctic provenance. Taken together, all of this suggests the classic scenario: penetration of the Andes by the *C. hecla* group in the Great American Interchange, followed by adaptive radiation and speciation. This fits the entire history of the Andean *Colias* into three million years.

Biochemical genetics ("molecular clocks") may give us a test of this scenario, if time points can be established to calibrate the rate of molecular evolution. In the meantime, it is not on its face unreasonable. The amount of morphological evolution in the Andean *Colias* is less than one routinely finds in exuberant insular lineages on similar time scales. Various plants whose occurence in the Andes has been attributed to the Great American Interchange have undergone substantial morphological change; there are woody Crucifers in northern Colombia and the world's largest lupine, *Lupinus paniculatus*, occurs in Peru, for example.

The biggest problem is *Colias ponteni*, also known as *C. imperialis*. It is the *Colias* allegedly from the Sandwich Islands (Hawaii) referred to in the quote from Dixey, above. It was put in its own genus, *Protocolias*, by Petersen (1963) on the basis of its remarkably primitive genitalia. Although it is indisputably the most primitive living (or recently extinct) *Colias*, no one really knows where it came from, and it has never been collected again. Shapiro (1993) tells its bizarre story. Gerardo Lamas (in litt.) believes the actual type locality was Cerro Tarn, near Port Famine, Magallanes (Chilean Patagonia). But this is in the heavily forested, perhumid part of the region, an unlikely *Colias* habitat. Another "Port Famine" butterfly, one actually collected by Darwin, was recently rediscovered in a different part of Magallanes in steppe, where it belongs (Herrera and Pérez d'A, 1989).

Biogeographers are perennially embarrassed by their inability to define criteria for identifying "centers of origin" (or to winnow the long list of contradictory criteria proposed by various authors). But by most such criteria, *Colias* should have originated in Laurasia, and the tip of South America is the last place to expect its center of origin. Thus *C. ponteni*, if truly Patagonian, must be rationalized away as a primitive species stranded in an out-of-the-way place and preserved (at least until the 1850s) by virtue of a lack of predators and competitors: a butterfly tuatara. But what of its relation (if any) to the other Andean *Colias*, and their Holarctic affinities?

To sum up: Descimon may be right, but declaring victory is decidedly premature. It would be very extraordinary if the entire Andean oreal fauna were of Holarctic origin. Just as even the far-north Andean oreal flora contains autochthonous elements (e.g., the Espeletiini, Compositae) as well as some derived from the lowlands — as noted by Descimon — so, too, the butterfly fauna is likely to be heterogeneous. The phenotypic convergences are so strong that biochemical-genetic and cladistic evi-

dence are absolutely necessary before any claim of homology can be accepted. As of now, there is no group, not even *Colias*, for which the claim of Holarctic origin can be considered fully established; and there is one — the hairstreaks — for which it has been virtually disproved.

The Pierids (Shapiro 1991a) and the blues, and perhaps *Colias*, all suggest ties to central Asia — presumably via a "Camelid scenario." Other groups that "should" partake of such a relationship are conspicuous by their absence in the Andes (*Lycaena*, *Parnassius*, various Holarctic Satyrids). Their absence alerts us to the possibility that the "ties" may not be real. Alternatively, the characteristic boreal-oreal fauna may not be as integrated a unit as we think.

The small Andean fritillaries (*Yramea*, Nymphalidae) have been linked with the small Holarctic ones (*Boloria*, *Clossiana*, *Brenthis*) and with the afro-tropical highland *Issoria*. Their true phylogenetic relationships are as yet unknown though two researchers (T. Pike and G. Lamas) are working on the problem. It now appears that the Austral *Yramea* feed on both Violaceae and Rosaceae (*Acaena*). This is precisely the pattern one finds in the boreal *Boloria*. The cynic will react to this news with a shrug and a "So what?"

BACK TO THE IMPOVERISHMENT

Why are the Andean-oreal faunas so impoverished? The question is not why the Sierran oreal fauna is so big, but why the Andean one is so small. As we have seen, the emerging Sierran oreal biota was recruited from more or less nearby sources with a history of dealing with increasingly harsh climates. In fact, the South American oreal biota was either recruited from nearby lowland tropical sources, with little or no history of dealing with such climates, or from a distant Holarctic biota, better adapted but with limited access — or some combination of both. Either way, severe hardships existed which would tend to limit the number of lineages able to establish themselves successfully in just a few million years at most. And either way, we would expect a nearly insular situation — full of "vacant niches" and offering grand evolutionary opportunities. As Descimon (1986, p. 520) states:

> The impression — subjective, of course — that is felt by a naturalist looking at the rhopaloceran fauna of the Andes is one of "unsaturation": many ecological niches appear "empty," in particular many food plants remain without insects... Many times, wandering in the Great Andes, I stopped to look at a peculiar-looking biotope, in which I guessed there surely were special — and interesting, perhaps new! -butterflies. And there were none.

As noted above, the prominent role of Holarctic plants in the Andean oreal flora would facilitate the establishment of Holarctic butterflies already associated with them. Descimon and I agree that host utilization in the Andes is very spotty, and both of us predict evolutionary radiation

onto new hosts if in fact the oreal fauna is young and in disequilibrium. In this regard, recent data on host utilization are very striking.

Given the host relationships of the Polyommatini in the Holarctic, it is perhaps not very surprising that at least four species of Andean blues have now been found breeding on species of the large and diversified Holarctic genus *Astragalus* (Shapiro, unpublished). This Papilionaceous Legume would be on most lists of Great American Interchange arrivals in the region. It is very surprising, however, to find Pierini eating these plants.

The ancestral hosts of the Holarctic Pierini are mustard-oil-containing plants. These compounds (glucosinolates) are found in the Cruciferae, Capparidaceae, Resedaceae and Tropaeolaceae. The first three are phylogenetically close, while the fourth is generally considered much more distantly if at all related. Most of the Andean Pierini reared so far (various *Tatochila* and *Hypsochila, Reliquia, Phulia, Pierphulia*) feed on Crucifers and/or Tropaeolaceae. The Crucifers have been considered Great American Interchange arrivals in the Andes; they have undergone much evolution especially in the north, but unfortunately their fossil record is essentially nil. They are absent from the lowland tropics, except as introduced weeds. Capparidaceae occur as shrubs in the xeric habitats of South America. Their habitats being fairly young, they may be also. Tropaeolaceae is an autochthonous Neotropical family, including both high-Andean and Patagonian taxa. If the ancestors of *Tatochila* and *Hypsochila* came south from the Nearctic, they presumably had chemically preadapted resources waiting for them. It now appears, however, that the genus *Tatochila* (as presently construed, almost certainly polyphyletic) has shifted from these plants onto Papilionaceous Legumes twice and perhaps three times, and the sister-genus *Hypsochila* at least once. The Legume genera involved are *Astragalus, Vicia, Lathyrus,* and (probably in the past century or so) *Trifolium.* In one case (*Tatochila distincta*) the animal can be reared successfully on Crucifers, but apparently only uses Legumes in nature. (See Shapiro, 1986, 1990, 1991b.)

This is an exceedingly odd pattern, insofar as no other Crucifer-feeding pierine anywhere else in the world has made such a switch despite plenty of sympatry with appropriate Legumes. No "chemical bridge" between the plant taxa has been recognized (which is not to say one may not occur). What is strangest, though, is the repeated colonization of one plant group derivative from the Nearctic from another. The case for adaptive radiation in host selection in the oreal biome would be much stronger if the move had been onto plants of tropical American or Austral affinity!

WHAT ABOUT PATAGONIA?

The Patagonian steppe is vegetationally and climatically reminiscent of the northern Great Basin desert of western North America, and for anyone who has worked in both areas, comparisons are inevitable.

The Patagonian butterfly fauna is exceedingly unbalanced, being dominated by the Pronophiline Satyrids. It is, however, fairly species-rich, and what is most striking is the fact that several of its lineages extend all the way to the northern Andes in the oreal biome. Yet, despite the climatic and vegetational diversity of this vast region, only a handful of species occur in the north, sometimes only one per lineage, while often several occur sympatrically in the south. Some of this may be merely an artifact of poor collecting in the Andes, and many of the Patagonian taxa, especially of Lycaenidae, are only very recently recognized. Moreover, the number of species is no reliable indicator of the "center of origin" for a genus, if such things can be inferred at all. Still, one gets the impression of groups that developed and radiated in the south and then moved north up the spine of the Andes, a pattern seemingly inconsistent with the bigger picture. It is not difficult to account for speciation in the south; the problem is to account for the lack of it in the north.

The high Andean-Patagonian connection is observed over a broad taxonomic spectrum. (See fig. 4.11 in Humphries and Parenti, 1986 and accompanying discussion; these authors give credence to a radical hypothesis — "Pacifica" — to account for it, but the timing would not work for butterflies. The postulated events are too early, requiring modern butterfly tribes to have differentiated in the Mesozoic.)

A peculiar problem affecting the blues, hairstreaks and pronophilini in Patagonia is very persistent convergence or stabilizing selection to the same color patterns — so that most of the hairstreaks found flying together look alike, even if not very closely related, and similarly for the Pronophilines. In both lineages there is a red blotch on the forewing underside, a theme found in some Holarctic Satyrids and in *Callipsyche behrii*, but never as a pervasive and defining trait of a whole fauna anywhere else!

The two major Satyrid lineages in South America are the Euptychiini, which are tropical and barely enter the temperate Argentine mid-latitudes, and the Pronophilini, which have speciated in two seeming bursts: one in the northern and central Andes associated with the Andean bamboos, the other in the *altiplano* and Patagonia on bunch-grasses. This second radiation is more diverse in lowland Argentina than in the Andean highlands (at both generic and specific levels). Some taxa, however, occur in both regions. The beautiful *Mariposa Plateada*, *Argyrophorus argenteus*, has a fascinating distribution which advertises Quaternary biotic movements. It occurs as relict local populations in the Chilean coast range and at high altitudes in the *cordillera* proper, in Coquimbo, San Juan, and Mendoza, thence south along the eastern foothills through the Uspallata Valley, to Aluminé, Zapala and Bariloche, reaching the immediate coast at Comodoro Rivadavia well south of its most austral inland outposts. Like the distribution of the Pierid *Tatochila theodice* (Shapiro, 1991b), this is in accord with the paleoclimatic reconstructions of Caviedes and Iriarte (1989) and Caviedes (1990). This work

envisions repeated north-south biotic migrations on both sides of the Andes, with movement sometimes from west to east and sometimes the reverse across the passes. Their model provides the best explanation of the Patagonian character of the Chilean Central Valley fauna. In the longer term, it implies the Patagonian butterfly fauna was already defined at the species level by the mid-Pleistocene, if not earlier. Unfortunately, these movements probably obliterated any biogeographic evidence bearing on the origins of that fauna -which may be approachable only molecularly or cladistically.

The Patagonian and Great Basin climates, and perhaps faunas, are probably of similar antiquity. Although the Patagonian fauna is much more unbalanced than the Great Basin one, insofar as it is dominated by Pronophilini, the overall species numbers are similar (Austin, 1985; Austin and Murphy, 1987). However fuzzy this statement, it certainly contrasts with the situation in the oreal zone. This once again forces us to think about why the Andean oreal fauna is so poor.

Coda

In 1968, Dunbar discussed the eco-evolutionary status of polar biotas and concluded that their impoverishment was probably due — in a variety of ways — to their geologic recency; they were both ecologically and evolutionarily immature, and the processes of maturation in both series were likely to be mutually reinforcing. The basic problems faced by an emerging polar biota are the same as those confronting the oreal butterfly fauna, except that seasonal extremes are replaced by diel ones. In this regard it is non-trivial that boreal butterfly faunas are consistently much richer than Andean oreal ones, and entrain a much broader selection of lineages from the source faunas. This almost certainly reflects the role of the periglacial environment, whence major elements of both our Arctic and alpine-oreal Holarctic biota derive. The character of this environment has been much debated — tundra, steppe-tundra, steppe (French 1976, Lamb and Edwards 1988, Pielou 1991) and it is worth noting that the butterflies whose ranges suggest derivation from it also suggest a dry tundra or steppe-tundra, as shown in the work of Kostrowicki (1969). The possibility of an equivalent antecedent in the *altiplano* or in Patagonia for the Andean oreal butterflies remains effectively unexplored. If there was none, that in itself might explain much about that fauna.

Whether the Andean oreal butterflies originated from the Holarctic or from the adjacent lowlands, their low diversity is very likely a function of time. If it turns out that the high Andes are much older than we have thought, however, the mystery, already deep, will become unfathomable.

Descimon for having the courage to take on these issues and to gather what scattered data there were bearing upon them. My own high-Andean work was benefitted from three NSF grants, most recently BSR-83-0692. My Sierran work has been underwritten mostly by California Agricultural Experiment Station Project CA-D*-AZO-3994, "Climatic Range Limitation of Phytophagous Lepidopterans." I thank Gerardo Lamas, Steve Courtney, Peggy Stern and José Herrera G. for much stimulating discussion and insight, and Hansjürg Geiger, Adam Porter, and Chris Nice for extraordinarily fruitful laboratory collaborations. The profound ignorance displayed herein is, however, all mine.

I dedicate the paper to the memory of José Herrera G., who recognized the problems very early, and of Adrienne Venables, who had she lived might have solved them.

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